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VOL. 23, SEC. D. OCTOBER, 1945 NUMBER 5

STUDIES ON CESTODES OF THE GENUS *TRIAENOPHORUS* FROM FISH OF LESSER SLAVE LAKE, ALBERTA

V. DESCRIPTION AND LIFE HISTORY OF *TRIAENOPHORUS STIZOSTEDIONIS* N.SP.[1]

BY RICHARD B. MILLER[2]

Abstract

Triaenophorus stizostedionis is a pseudophyllidean cestode that occurs as an adult in the intestine of the pike-perch, *Stizostedion vitreum*. It differs from *T. crassus* and *T. nodulosus* in several morphological characters but particularly in the shape of the scolex hooks and the size and disposition of the male genitalia. Sexual maturity is attained in the spring; spawning and death take place during the first two weeks of June. The eggs average 56 μ long by 40 μ wide. The coracidia average 73 by 71 μ. The procercoid develops in the copepod, *Cyclops bicuspidatus*, in from 10 days to two weeks. When fully grown it reaches 220 μ. The plerocercoids occur encysted on the visceral and parietal peritoneum of the trout-perch, *Percopsis omiscomaycus*. The life history is completed when an infested trout-perch is swallowed by a pike-perch.

During the course of several summers' study of *Triaenophorus crassus* Forel and *T. nodulosus* (Pallas), a third type of *Triaenophorus* was encountered in the intestine of the pike-perch*, *Stizostedion vitreum* (Mitchill). This cestode is very similar to the other two species. The scolex is large, like that of *T. crassus*, but the hooks are small, like those of *T. nodulosus*. A close study revealed morphological differences in the genitalia. It was concluded that this must be a distinct species. In searching the literature for a description of this worm Cooper's account (1) of a *Triaenophorus* from *Stizostedion* was found. Cooper assigned his specimens to *nodulosus* but remarked that they appeared a sort of compromise between *crassus* and *nodulosus*. Cooper's specimens, which were immature, came from pike-perch of Lake Michigan. The present writer found these parasites in pike-perch taken from Lake Superior near Duluth. It seems fairly certain that this species, here described under the specific name *stizostedionis*, is the same as the worms mentioned by Cooper.

Description of Mature Adult

The species possesses the characters of the genus *Triaenophorus* Rudolphi (9).

[1] *Manuscript received May 14, 1945.*
Contribution from the Department of Zoology, University of Alberta, Edmonton, Alta.

[2] *Assistant Professor of Zoology.*

* *The name pickerel was used for the same fish in Part I of these studies. Although this is a familiar and widely used term it is not strictly correct and, at the suggestion of Professor J. R. Dymond, the author has agreed to use the correct name of pike-perch.*

The mature adult varies from 120 to 380 mm. in length and two to four mm. in width. It is longer than *T. nodulosus* (70-270 mm.) and shorter than *T. crassus* (130-400 mm.) (4).

The scolex (Figs. 1, 2, and 3) is broadly oval in surficial view; the bothria are deep and conspicuous; they are round and average 422 μ in diameter.

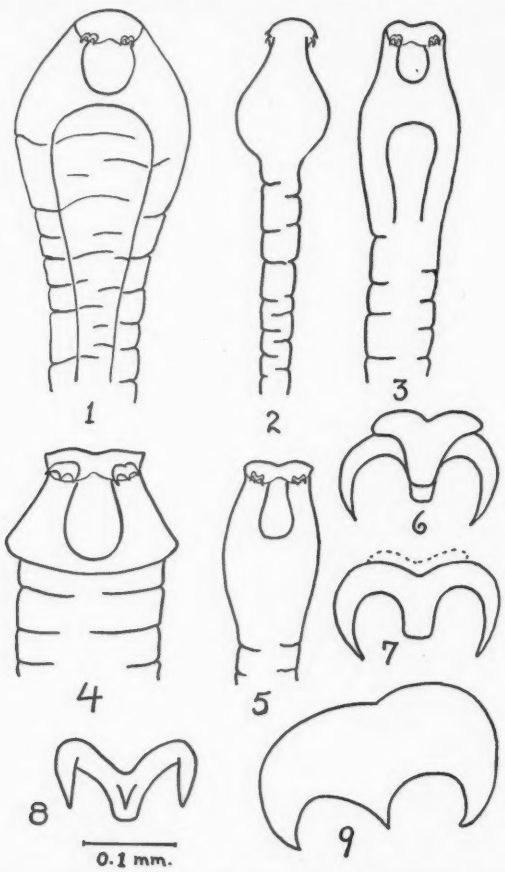

FIG. 1. *The scolex of a ripe specimen of Triaenophorus stizostedionis, surficial view.*
FIG. 2. *The same, lateral view.*
FIG. 3. *Scolex of an immature adult of Triaenophorus stizostedionis, surficial view.*
FIG. 4. *The scolex of T. crassus, surficial view.*
FIG. 5. *The scolex of T. nodulosus, surficial view.*
FIG. 6. *Camera lucida drawing of a scolex hook of T. stizostedionis, medial surface.*
FIG. 7. *The same, lateral surface. The dotted line represents a portion of the hook that is frequently not visible in whole mounts.*
FIG. 8. *Camera lucida drawing of a scolex hook of T. nodulosus.*
FIG. 9. *Camera lucida drawing of a scolex hook of T. crassus.*
NOTE.—*The 0.1 mm. line applies to Figs. 6-9.*

The terminal disk bearing the hooks is distinct, especially in marginal view. The posterior margins of the bothria are raised to form distinct ridges (Fig. 2), best seen in side view. The scolex of young individuals (Fig. 3) is slight and unexpanded and closely resembles that of *T. nodulosus* (Fig. 5). In older specimens the scolex and the first part of the strobila become greatly expanded so that the whole structure is more like the scolex of *T. crassus* (Fig. 4) but lacks the annular thickening at the base. The hinder part of the scolex and the anterior part of the strobila are broad and strongly biconcave. Comparative scolex measurements of the three species are given in Table I.

TABLE I

SCOLEX MEASUREMENTS OF *T. crassus*, *T. nodulosus*, AND *T. stizostedionis* (mm.)

Species	Length	Width of terminal disk	Width posteriorly	Authority
T. crassus	0.98–1.12	0.77–0.84	1.05–1.30	Cooper (1)
T. crassus	0.92–1.29	0.67–0.92	0.92–1.38	Hjortland (3)
T. nodulosus	0.55–0.92	0.35–0.42	0.26–0.64	Cooper (1)
T. nodulosus	0.44–0.62	0.30–0.35	0.53–0.72	Present paper
T. stizostedionis	0.53–1.14	0.62–0.88	1.06–1.94	Present paper

The scolex hooks of *T. stizostedionis* are characteristic. Each consists of a narrow, curved basal plate, which bears three prongs. The median prong is stout and, with the basal plate, is embedded in the tissue of the scolex. The two marginal prongs are longer; they are curved, slender, and project free from the scolex. The fourth projection, characteristic of *T. nodulosus* (Fig. 8) is lacking. On its mesial surface each hook has a somewhat Y-shaped protuberance (Fig. 6), which is difficult to see unless the hook is dissected off the scolex. In Fig. 7 the part shown in dotted lines is the portion of this protuberance that can sometimes be seen in surficial view of a living or fresh specimen. This protuberance is alone sufficient to distinguish *T. stizostedionis* from *T. crassus* (Fig. 9) or *T. nodulosus* (Fig. 8). In Table II comparative measurements of the hooks of the three species are given.

TABLE II

DIMENSIONS OF THE SCOLEX HOOKS OF *T. crassus*, *T. nodulosus*, AND *T. stizostedionis* (μ)

Species	Width of basal plate	Depth of basal plate (anterior–posterior)	Length of marginal prong	Authority
T. crassus	285–300	125–135	240–255	Scheuring (10)
T. crassus	275	138	245	Ekbaum (2)
T. crassus	255–300	132–140	—	Miller (4)
T. crassus	280–310	—	—	Cooper (1)
T. nodulosus	90–140	23–45	45–75	Scheuring (10)
T. nodulosus	112–120	20–30	—	Miller (4)
T. nodulosus	130–190	—	—	Cooper (1)
T. stizostedionis	123–198	22–33	48–77	Present paper
Average	150	28	68	Present paper

The genital organs agree in general with those of *T. crassus* described by Hjortland (3). The genital pores are marginal and alternate irregularly as in the other two species. Fig. 10 is a camera lucida sketch of the sex organs of *T. stizostedionis* exclusive of the testes and vitellaria. The figure shows the typical triaenophorine arrangement and is published because the only

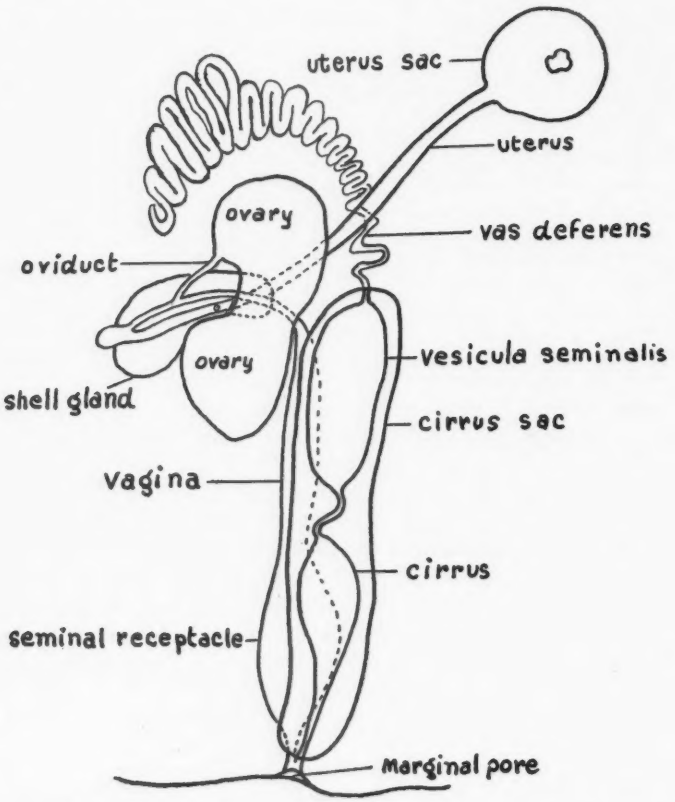

FIG. 10. *Camera lucida sketch of the genital organs (exclusive of vitellaria and testes) of a mature specimen of T. stizostedionis, ventral aspect. Certain of the details of the ducts have been supplied from serial sections. The small circle near the beginning of the uterus marks the point of discharge of the yolk reservoir.* × 110.

other in the North American literature, that of Newton (8), differs considerably from the author's findings.

The testes (Fig. 11) occur in the medullary parenchyma; they vary in diameter from 62-114 μ; those of *T. nodulosus* are from 57-88 μ and those of *T. crassus* (3), from 64-72 μ.

The vasa efferentia were not observed.

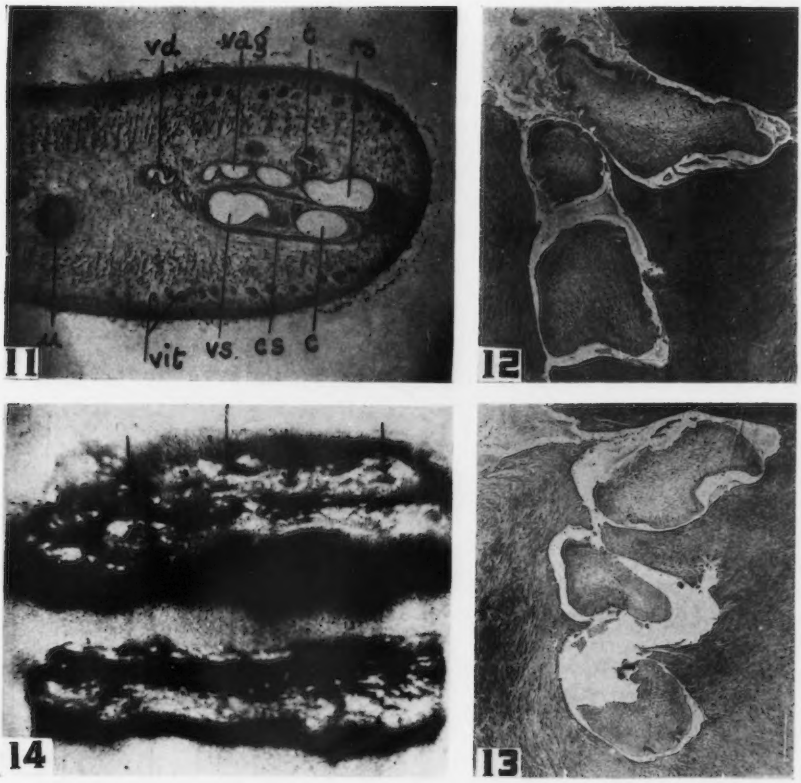

FIG. 11. *Photomicrograph of a portion of a transverse section through a mature proglottis of T. stizostedionis.* × *51. C = cirrus; cs = cirrus sac; rs = receptaculum seminis (?); t = testes; u = uterus; vag = vagina; vd = vas deferens; vit = vitellaria; vs = vesicula seminalis interna.*

FIG. 12. *Photomicrograph of a section through the intestine of a pike-perch at the common point of attachment of three individuals of T. stizostedionis.* × *15.*

FIG. 13. *The same at a different level to show how the scolices of the worms diverge to individual pits.* × 15.

FIG. 14. *Photograph of the split intestines of two pike-perch of the same size; the upper was parasitized with T. stizostedionis and the pits made by the worms are indicated by arrows; the lower was not parasitized. Less than natural size; enlarged from 16 mm. negative.*

The vas deferens (Fig. 10) is a long, strongly coiled tube occupying the central region of the medullary parenchyma. The coiling becomes less as it nears the cirrus sac. On entering this structure it dilates to form a large and conspicuous vesicula seminalis interna (Figs. 10 and 11). It and a portion of the vas deferens are ciliated. In his description of *T. crassus*, Hjortland (3) failed to mention this structure. Measurements at its maximum size in fully matured proglottids of each of the three species are as follows,—

T. stizostedionis—264 μ long by 88 μ wide,
T. nodulosus—400 μ long by 282 μ wide,
T. crassus—158 μ long by 158 μ wide.

The vesicula seminalis interna is of considerable taxonomic value. It is small and spherical in *T. crassus;* in *T. nodulosus* it is very large and broadly oval; in *T. stizostedionis* it is large and cylindrical, i.e., more than twice as long as its width.

The cirrus (Figs. 10 and 11) leads out of the vesicula seminalis interna. Its proximal part is narrow and has a single coil; the distal part is dilated to a width of 88 μ and then narrowed again at its external opening to 26 μ. The protruded cirrus is rarely seen; it is mushroom-shaped, 40 μ long and 88 μ broad; low, indistinct papillae cover its exposed surface.

The cirrus sac (Figs. 10 and 11) is a transversely elongated pouch with an average length of 616 μ in mature proglottids. Comparative measurements of the cirrus sac of the three species are given in Table III.

TABLE III

CIRRUS SAC LENGTH IN MATURE PROGLOTTIDS OF *Triaenophorus stizostedionis*, *T. nodulosus*, AND *T. crassus* (μ)

Species	Average	Range	Percentage of proglottis width
T. stizostedionis	616	493–704	32–37
T. crassus	704	581–739	40–47
T. nodulosus	827	739–968	47–66

The cirrus sac provides a useful and fool-proof taxonomic character. In actual size and in size relative to the proglottis width it is smallest in *T. stizostedionis;* in this species it fails to reach the level of the uterine sac (Fig. 10). In *T. nodulosus* the cirrus sac is actually and relatively largest and in *T. crassus* it is of intermediate size. In ripe proglottids the cirrus sac becomes greatly distended proximally owing to the dilation of the vesicula seminalis interna.

The above distinctions in the male genitalia (cirrus sac, vesicula seminalis interna) between *T. crassus* and *T. nodulosus* strengthen the author's (4) and Ekbaum's (2) conclusions that Wardle (11) was mistaken in judging these two cestodes to be but morphae of a single species.

The ovary is a bilobed structure; the two lobes are connected by a narrower bridge (Fig. 10). It occurs in the medullary parenchyma slightly toward the side on which the genital ducts open. The widths of the ovary in the three species at comparable stages of maturity are,—

T. stizostedionis, 317-387 μ; average, 354 μ.
T. crassus, 387-440 μ; average, 404 μ.
T. nodulosus, 202-238 μ; average, 218 μ.

In ripe specimens (uterus filled with eggs) the ovary grows considerably larger.

The vitellaria (Fig. 11) are numerous, small, scattered follicles in the cortical parenchyma. In *T. stizostedionis* they range from 37-53 μ in diameter; in *T. crassus* they are about the same size; in *T. nodulosus* they are larger, from 57-110 μ in diameter.

The vitelline ducts were not determined with sufficient clarity to permit description.

The yolk reservoir, which receives the vitelline ducts, measures 66 μ by 26 μ; its long axis lies in the dorsoventral plane. It discharges dorsally into the portion of the oviduct passing through the shell gland (see small circle in Fig. 10).

The oviduct, shell gland, and uterus (Fig. 10) agree with Hjortland's description of *T. crassus*.

The vagina, contrary to Hjortland's account, opens dorsal to the cirrus in all three species. In *T. stizostedionis* it measures 31 μ in diameter at its opening; it soon dilates to a large chamber, possibly a receptaculum seminis (Figs. 10 and 11), measuring 176 μ by 100 μ in diameter. As it nears the oviduct it becomes progressively smaller and in the region of the ovary and shell gland it measures only 17-18 μ in diameter. No indication of a receptaculum seminis was found in the ovary region of the vagina.

The type specimen is a whole mount in the author's collection, catalogue No. 42-82, collected from a pike-perch at Lesser Slave Lake, May 11, 1942. Numerous additional specimens are in the same collection.

Life of the Adult in the Pike-Perch

The adult of *T. stizostedionis* has been found only in the pike-perch, *Stizostedion vitreum*. The author has found this species in pike-perch from Lake Superior and in a collection from Great Slave Lake made by Dr. D. S. Rawson, as well as in Lesser Slave Lake.

The worms always occur in the few inches of intestine just distal to the pyloric sphincter. Their scolices are deeply embedded in pits in the gut wall. The pits widen distally to accommodate the expanded scolex making it difficult to pull the worms out without breaking them. Very often several pits occur so close together that they share one opening into the lumen of the

gut. Thus, in one pike-perch examined, 24 pits accommodated 75 worms, from two to four parasites protruded from each pit; dissection revealed the scolices embedded in separate pits that branched off from the main one. Figs. 12 and 13 are photomicrographs of sections through a pit in which three scolices are embedded. This 'communal' tendency of *T. stizostedionis* distinguishes it from *T. crassus* and *T. nodulosus*, which always occupy solitary pits in their host's gut.

The host gut reacts considerably to the presence of the parasites. Figs. 12 and 13 show how the mucosa is destroyed and the gut wall thickened. Measurements of fresh specimens showed that whereas the normal thickness of the intestinal wall is 2-3 mm., in parasitized regions it is 7 mm. thick. It is easy to recognize parasitized intestines, without opening them, by their increased size. The outside diameter of an infested intestine reaches 14-15 mm. while it is only 5-6 mm. in a clean fish. Fig. 14 shows photographs of an infested and non-infested intestine, both split open and the worms removed. The pits where the worms were attached are easily distinguished.

The number of parasites per host varied from one to 75; the average was approximately 10 per fish. The pike-perch of Lesser Slave Lake were 58.6% infested.

The worms mature in late spring. Table IV presents a summary of the observations on time of ripening and egg release.

TABLE IV

SEASONAL VARIATION IN NUMBERS AND THE STATE OF THE SEX ORGANS IN *T. stizostedionis*

Date	Number of pike-perch examined	Number of pike-perch parasitized*	Condition of parasites
1942			
May 11-15	7	6	Firmly embedded in gut; eggs not released in water; no formed coracidia
May 16-31	14	7	Firmly embedded in gut; eggs released in water; no formed coracidia
June 1-15	32	9 (4)*	Loose and leaving gut; eggs with formed coracidia; some new infection
June 16-30	10	3	Empty pits healing up; new infection, lightly attached to gut
1943			
May 20 and 21	8	3	Firmly embedded in gut; eggs not released in water; no formed coracidia
June 19-28	16	2 (2)	One releasing eggs; one new infection

** Numbers in parentheses represent fish that had no worms but empty pits in their intestinal walls showed that worms had recently been present.*

From Table IV it can be seen that the main spawning period is during the first two weeks in June, one month later than *T. crassus* (May 1-14) and one to two weeks later than *T. nodulosus* (May 24-June 6) (4).

As the time of egg-laying approaches the scolices loosen in their pits and finally they pull out; often the strobilae break into fragments. Eventually the whole worm escapes through the anus into the water. The majority of the eggs are released on contact with the water; they burst from the uteri in clouds more or less simultaneously along the length of the strobila. Soon the shrunken strobilae sink to the bottom and die.

New infection commonly appears about the same time so that pike-perch are never completely free of these parasites as pike are of *T. crassus* and *T. nodulosus* (4).

The Eggs and Coracidia

The eggs of *Triaenophorus stizostedionis* are at first white in colour, but turn brown after an hour and a half in water. The average size is 56 μ by 40 μ; the largest egg measured was 62 μ by 46 μ; the smallest 53 μ by 37 μ. (Average egg size for *T. nodulosus* and *T. crassus*, 61 μ by 44 μ (4)).

Many eggs were reared in Petri dishes in the field laboratory. The hatching records of four such cultures are shown in Table V.

TABLE V

THE HATCHING OF FOUR CULTURES OF EGGS OF *Triaenophorus stizostedionis*

Culture No.	%	Days after beginning of hatching											
		0	1	2	3	4	5	6	7	8	9	10	11
1	Hatched	3	9	32	54	58	83	84	85	—	—	—	—
	Coracidia alive	—	70	—	—	20	—	2	0	—	—	—	—
2	Hatched	4	24	57	70	77	84	80	—	85	85	85	85
	Coracidia alive	100	100	70	60	—	10	5	—	—	2	—	0
3	Hatched	6	18	55	75	85	75	81	80	—	—	—	—
	Coracidia alive	100	71	85	65	54	22	6	0	—	—	—	—
4	Hatched	0.1	6	8	3	9	16	53	68	—	85	85	—
	Coracidia alive	100	100	90	67	65	30	25	5	—	1	0	—

Hatching lasts for one week; 85% of the eggs hatched; the remainder appeared to be infertile. Hatching is the same as described for *T. crassus* and *T. nodulosus* (5).

As in *T. crassus* and *T. nodulosus* the coracidia survive for at most two days after hatching.

The coracidia reach their maximum size about 24 hr. after hatching. They then average 73 μ long by 72 μ wide. The largest measured was 101 μ by 88 μ and the smallest 53 μ by 48 μ. Coracidia of *T. crassus* average 73 μ by 54 μ and of *T. nodulosus*, 75 μ by 60 μ (5). The coracidia of *T. stizostedionis* are more nearly spherical than those of *T. crassus* and *T. nodulosus* but are very similar in every other respect.

The Procercoid and the First Intermediate Host

Laboratory cultures of *Cyclops bicuspidatus* Claus were very easily infected with coracidia of *T. stizostedionis*. A search for other possible copepod hosts was not made.

Less than one hour after introducing them to the copepod culture the coracidia were found in the stomachs of *Cyclops* digging through the stomach walls with their hooks. In a few hours most of the parasites were in the body cavity. Their subsequent growth was observed in two cultures; the data are summarized in Table VI.

TABLE VI

THE GROWTH OF PROCERCOIDS OF *Triaenophorus stizostedionis* IN THE BODY CAVITY OF *Cyclops bicuspidatus*. MEASUREMENTS IN μ

Culture No.	——	Days after contact of coracidia and *Cyclops*									
		0	1	2	5	6	7	9	10	11	13
1	Av. length	33	42	53	70	—	66	92	—	101	92
	Max. length	44	48	75	73	—	88	198	—	119	198*
	Av. no./*Cyclops*	4	9.5	13.3	8	—	15	11	—	8	11
2	Av. length	—	—	—	—	112	—	—	220	—	—
	Max. length	—	—	—	—	114	—	—	220*	—	—
	Av. no./*Cyclops*	—	—	—	—	2	—	—	1	—	—

* *With a cercomere developed.*

The procercoid reaches its full growth in the *Cyclops* in from 10 days to two weeks. Table VI shows that a larger size in shorter time is attained when fewer procercoids occur in each *Cyclops*. The largest procercoid observed was 220 μ long including the cercomere, which measured 5 μ. The procercoids of *T. stizostedionis*, though smaller than those of *T. crassus* and *T. nodulosus*, are similar in every respect with the possible exception of the cercomere, which tends to be somewhat more spherical.

The above findings show that *Cyclops bicuspidatus* carrying mature procercoids of *T. stizostedionis* would be present in the lake from the middle to the end of June.

The Plerocercoid and the Second Intermediate Host

No attempt was made to discover the second intermediate host by feeding experiments or to observe the transition from procercoid to plerocercoid. The investigation was confined to a search for encysted plerocercoids with scolices similar to the adult of *T. stizostedionis*. Such plerocercoids were found in the trout-perch, *Percopsis omiscomaycus* (Walbaum).

Adults and juveniles of the following species were examined with negative results,—*Notropis hudsonius* (Clinton), *N. atherinoides* Rafinesque, *Catostomus commersonnii* (Lacépède), *C. catostomus* (Forster), *Lota lota maculosa* (Le Sueur), *Perca flavescens* (Mitchill), *Esox lucius* Linnaeus, *Leucichthys* spp., and *Coregonus clupeaformis* (Mitchill).

The material from trout-perch is, unfortunately, rather scanty owing to the difficulty experienced in catching many of these fish. Altogether only 53 were examined; these were obtained in a small creek during their annual spawning run toward the end of June and early in July. Of these, 14 or 26.4% were parasitized with a total of 19 cysts of *T. stizostedionis*. The 19 cysts were disposed as follows, six attached to the visceral peritoneum of the liver, 11 attached to the pyloric caeca and two to the gonads. All the cysts protruded into the coelom from their points of attachment; none was wholly within an organ like *T. nodulosus* in the burbot liver or *T. crassus* in the flesh of coregonine fishes.

The cysts ranged from 2-11 mm. in length, average 4 mm. They were roughly spherical. They consist of a whitish to yellowish fibrous wall enclosing a thick liquid and the coiled plerocercoid, exactly as the cysts of the two other species.

One cyst contained two plerocercoids.

The plerocercoids possessed scolices identical with those of young adults. The strobilae were slender and showed no trace of sex organs. They ranged from 5-28 mm. in length, average 16 mm.

Half the plerocercoids were provided with a cauda that made up from 40 to 50% of the total length. In accordance with the author's views (4, 7) that the cauda is a product of the progressive degeneration of the strobila from the posterior end, these plerocercoids with caudae were interpreted as two- or three-year-olds, and those without caudae were regarded as the current year's infestation.

No feeding experiments were carried out with these cysts. However, the stomach contents of many pike-perch were examined and trout-perch were found to compose the largest single item of food taken during June and July. Many pike-perch were taken that had several trout-perch in their stomachs. Thus it is a natural and frequent occurrence for pike-perch to swallow encysted plerocercoids of *Triaenophorus stizostedionis*.

Discussion

The three species of *Triaenophorus* whose life histories have been described in this paper and the four (4, 5, 6, and 7) that preceded it offer an interesting picture of a stage in the evolution of species. That the three species are very closely related is obvious from morphological studies. Their sex organs are similar in general plan and differ only in details. Their scolices are fundamentally the same and are distinguishable only by virtue of small differences in their armatures. If these species had identical life histories they would possibly be regarded as subspecies or varieties rather than true species.

Even in life history details there is considerable similarity. *T. crassus* and *T. nodulosus* share the same definitive host, *Esox lucius*. *T. stizostedionis* has a different adult host but shares with the other two the same first intermediate host, *Cyclops bicuspidatus*. The greatest diversity is found in the second intermediate host, which is different for each species.

The differences possibly arose from a gradual lengthening of the spawning period of the original or ancestral species. This would give an equally long period when coracidia were present in the water. The first intermediate host, *Cyclops bicuspidatus*, which swallows these coracidia, is abundantly present at all seasons of open water. The lengthened spawning period would have no effect on this phase of the life history. But the fishes that frequent shallow water in the spring and early summer (the period when parasitized *Cyclops* would be available) are by no means constant. In early spring the coregonine fishes (whitefish and tullibee) are in shallow water and therefore available as second intermediate hosts. Later in the spring, perch and burbot are more abundant and the coregonines have left for deeper water. Trout-perch stay out from shore until their spawning season in late June and early July. Thus the earliest procercoids would be swallowed mainly by whitefish and tullibees; later ones would go largely to perch and burbot; the latest appearing procercoids would find trout-perch by which they could be swallowed.

The three species of *Triaenophorus* spawn in Lesser Slave Lake as follows,—

T. crassus—May 1 to May 14,

T. nodulosus—May 24 to June 6,

T. stizostedionis—June 1 to June 15.

They form a series beginning in early May and extending to mid-June. It is possible, therefore, that they together represent the long spawning period of an ancestral species broken into three species in the course of time owing to the different species of fishes available as second intermediate hosts.

The change of adult host in *T. stizostedionis* from pike to pike-perch is possibly the result of the tendency of pike-perch to feed on trout-perch more consistently than pike do.

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